

SEASONAL BIRD USE OF CANOPY GAPS IN A BOTTOMLAND FOREST

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ABSTRACT.—Bird use of small canopy gaps within mature forests has not been well studied, particularly across multiple seasons. We investigated seasonal differences in bird use of gap and forest habitat within a bottomland hardwood forest in the Upper Coastal Plain of South Carolina. Gaps were 0.13- to 0.5-ha, 7- to 8-year-old group-selection timber harvest openings. Our study occurred during four bird-use periods (spring migration, breeding, postbreeding, and fall migration) in 2001 and 2002. We used plot counts and mist netting to estimate bird abundance in canopy gaps and surrounding mature forest habitats. Using both survey methods, we observed more birds, including forest-interior species, forest-edge species, field-edge species, and several individual species in canopy gap and gap-edge habitats than in surrounding mature forest during all periods. Interactions between period and habitat type often were significant in models, suggesting a seasonal shift in habitat use. Bird activity generally shifted between the interior of canopy gaps and the immediate gap edge, but many species increased their use of forested habitat during the breeding period. This suggests that many species of birds selectively choose gap and gap-edge habitat over surrounding mature forest during the non-breeding period. Creation of small canopy gaps within a mature forest may increase local bird species richness. The reasons for increased bird activity in gaps remain unclear. *Received 8 August 2005. Accepted 12 July 2006.*

Many species of birds, including several species of conservation concern that breed in mature forests, require some amount of forest disturbance to create ideal habitat (Hunter et al. 2001). One type of disturbance common in mature forests occurs when trees fall from fire, ice, wind, or insect damage creating small light gaps in the forest canopy. Such gaps provide microclimates and habitat patches that lead to a unique assortment of gap-associated flora and fauna (Watt 1947, Canham et al. 1990), and increase the heterogeneity of vegetation structure in the forest. Canopy gaps created by small-scale timber harvest operations may mimic these natural disturbances.

Birds select habitat based largely upon vegetation structure (Holmes et al. 1979), and some may prefer early successional gap habitat based on the unique qualities of the vegetation (e.g., dense foliage, well-developed herb and shrub layer). Several bird species seem to prefer small-scale canopy gap openings to mature forested habitat during migration or the breeding period (Martin and Karr 1986, Germaine et al. 1997, Kilgo et al. 1999,

Moorman and Guynn 2001). Forest canopy gaps may be used differently throughout the year, depending on the availability of protective cover, desirable nesting habitat, or suitable prey items (Robinson and Holmes 1982, Willson et al. 1982, Blake and Hoppes 1986). During migration, birds pass through unfamiliar habitats and tend not to spend much time in any one location (Moore et al. 1993). Habitat selection during these periods may be influenced by available food resources, competition with other species, and risk of predation (Petit 2000). During the breeding period, birds require habitat with suitable nesting sites. Birds that breed in early successional habitats, including Common Yellowthroat and Indigo Bunting (scientific names in Appendix), use regenerating canopy gaps for nesting (Moorman and Guynn 2001). During the post-breeding period, adults may select densely vegetated habitats as refugia while molting (Vega Rivera et al. 1999), and young may seek the protective cover from predators offered by gaps (Anders et al. 1998, Vega Rivera et al. 1998), as each group is particularly vulnerable at that time.

Seasonal variation in the use of artificial, small-scale disturbances by birds within mature forests has not been well studied, and no research has systematically addressed the relative use of gap habitat throughout the growing season, beginning with spring migration

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and ending with fall migration. Our goal was to examine relative use of gap and forest habitat by birds through four periods (spring, breeding, postbreeding, and fall) within a bottomland hardwood forest to provide a more comprehensive assessment of the response of forest birds to canopy gaps. We hypothesized that relative bird use of gaps would be highest during the non-breeding period when dense vegetative cover is important to dispersing and migrating individuals.

METHODS

Study Area.—We studied birds during 2001 and 2002 at the Savannah River Site (33° 09' N, 81° 40' W), a 78,000-ha National Environmental Research Park owned and operated by the U.S. Department of Energy. Our study site was a mature stand of bottomland hardwoods approximately 120 ha in size in Barnwell County in the Upper Coastal Plain of South Carolina. We surveyed birds in 12 group-selection gaps harvested in December 1994 and in the mature forest adjacent to gaps. Gaps were of three sizes (0.13, 0.26, and 0.50 ha) with four replicates of each size. It is within this size range that previous research has identified a threshold in response by breeding (Moorman and Guynn 2001) and fall migrant birds (Kilgo et al. 1999). The mature forest canopy was dominated by laurel oak (*Quercus laurifolia*), cherrybark oak (*Q. falcata* var. *pagodaefolia*), sweetgum (*Liquidambar styraciflua*), and loblolly pine (*Pinus taeda*). The midstory was poorly developed, consisting primarily of red mulberry (*Morus rubra*), ironwood (*Carpinus carolinianus*), and American holly (*Ilex opaca*). The understory was dominated by dwarf palmetto (*Sabal minor*) and switchcane (*Arundinaria gigantea*). Vegetation in the gaps was approximately 1–8 m in height and was dominated by regenerating trees (primarily sweetgum, loblolly pine, sycamore [*Platanus occidentalis*], green ash [*Fraxinus pennsylvanica*], oaks, and black willow [*Salix nigra*]), and dense stands of blackberry (*Rubus* spp.), dwarf palmetto, and switchcane.

Bird Surveys.—We surveyed birds each year during four avian activity periods: spring migration (25 Mar through 15 May), breeding (16 May through 30 Jun), postbreeding (1 Jul through 31 Aug), and fall migration (1 Sep

through 18 Oct). These beginning and ending dates are estimates of biologically meaningful periods, but each overlaps extensively with the other. Although many individuals initiated breeding on our study area before 16 May, transient species that breed to the north continued to migrate through South Carolina until mid-May. Similarly, some individuals migrated from or through our study area before 1 September, but the bulk of fall migration occurred after 1 September.

Plot counts were conducted within each of the 12 experimental gaps and within 12 forested control plots of equivalent size. The 12 forested control plots were randomly placed a minimum of 100 m from the nearest gap center within the mature forest surrounding the study gaps. The forest plot perimeters were flagged so that observers could easily identify plot boundaries. Each of the 24 plots was visited three times during each period and counts were averaged over the three visits. For approximately one half of the plot counts and equally distributed across treatment types, two observers walked slowly around the perimeter of each plot, recording all birds seen and heard. When the observers met on the opposite side of the plot, they compared observations and agreed upon a total number for each bird species observed within the gap-edge habitat. When only one observer was available, the single observer walked slowly around the entire plot. At both forest and gap plots, birds observed within the actual plot and at the immediate edge (0–10 m from the bole line or flagged boundary into the forest) were included in the count. Surveys varied widely in length (15 to 45 min); larger plots and plots with more bird activity took longer to survey. The percentage of gap habitat in plot counts increased as gap size increased. However, the effect of gap size on bird use was not significant ($P > 0.05$) and we did not include the variable in our models.

At each of the 12 study gaps, we placed three constant effort mist-net stations along a line emanating southward from the gap center: one at the approximate gap center, one at the gap edge perpendicular to and bisecting the tree line, and one 50 m into the surrounding forest. The interior gap mist net was a proxy for gap abundance, the gap-edge net was a proxy for edge abundance, and the 50-m-into-

the-forest net was a proxy for forest abundance. During the spring migration, post-breeding, and fall migration periods, netting was conducted once each week at each gap, rotating among gaps on a regular weekly schedule. During the breeding period, nets were operated once every 2 weeks because birds tend to remain fairly stationary during this period. Nets were opened at first light and operated for 4–6 hrs, depending on daily weather conditions. Netting was not conducted when wind exceeded 16 km/hr or during steady rainfall. Nets were 12 m long $\times$ 3 m tall, with 30-mm mesh. Captured birds were classified to age and gender (Pyle 1997), weighed, and banded with a federal aluminum leg band. We operated mist nets for a total of 7,669 net hrs over the 2 years of the study.

Mist-net surveys and plot counts were not meant to be directly comparable, but rather separate, distinct measures of bird use of gap and adjacent forest habitat in each of four bird-use periods. Plot counts at gap sites included both gap and edge habitat, so the percentage of bird use of gap *per se* versus the first 10 m of forest (i.e., the edge) could not be measured seasonally as it could for mist-net captures. We chose not to note whether birds specifically were recorded in the 10-m outer band of gap and control plot counts because birds often moved back and forth across the boundary as they foraged. Additionally, we were most interested in bird use of gap-edge habitat compared to an equal size area of mature forest. Finally, forest mist-net stations were not placed with control plot count circles because the best location (i.e., at least 100 m from the nearest gap center) for plot counts frequently did not lie along the southward emanating mist-net transect. Mist nets and plot counts each have their limitations, but the combined use of the two sampling techniques allowed us to more comprehensively measure bird use of the gaps and adjacent mature forest.

Statistical Analyses.—We used a linear mixed model (PROC MIXED, SAS Institute, Inc. 1990) to perform repeated measures ANOVA comparing the effects of habitat type, period, and the interaction between habitat and period on bird abundance. We used mean birds per ha as the dependent variable for plot count analyses and mean captures per 100 net

hrs as the dependent variable for mist-netting analyses. For plot count data analysis, habitats included gap-edge and forest; for mist-netting data analysis, habitats included gap, edge, and forest. We considered habitat type and period as fixed effects, with habitat type as a split plot factor and period as the repeated measure. We used the test for the habitat $\times$ period interaction to assess whether habitat use was consistent across periods (i.e., an interaction between the two variables indicated that relative use of the habitats differed among the periods). Significant interactions generally were the result of varying extents of differences among gap, edge, and forest use but in a consistent direction across periods. We interpreted period and habitat effects separately even when there was an interaction between the two variables. Years were not significant ($P > 0.05$) in any model and were pooled in the final analyses. These pooled data are represented in tables and figures.

We assigned birds to habitat-use groups (Appendix): (1) all birds, (2) forest-interior species, (3) forest-edge species, and (4) field-edge species (Ehrlich et al. 1988, Hamel 1992). We analyzed mist-netting captures and plot count detections for each group. Individual species were chosen for analysis if they accounted for at least 80 detections over both years for plot counts (Blue-gray Gnatcatcher, Carolina Wren, Tufted Titmouse, Northern Cardinal, Northern Parula, and White-eyed Vireo) or at least 80 captures over both years for mist netting (Black-throated Blue Warbler, Carolina Wren, Hooded Warbler, Kentucky Warbler, Northern Cardinal, and White-eyed Vireo). We included species that bred at our study site and transient migrants that bred to the north in our analyses. Birds considered winter residents, present only in early spring or late fall, were not included.

RESULTS

Plot Counts.—From April through October in 2001 and 2002, we counted 1,711 individuals representing 70 species in gap-edge habitat and 38 species in forest habitat. We detected more individuals in the gaps than in the surrounding forest during all periods for all bird groups and individual species analyzed (Table 1, Fig. 1). The abundance of forest-interior birds, field-edge birds, Blue-gray

TABLE 1. Effects of period (spring migration, breeding, postbreeding, fall migration), habitat (gap-edge and forest), and the period $\times$ habitat interaction (ANOVA) on abundance of bird species/groups detected on plot counts of gaps and forest areas in a bottomland hardwood forest in South Carolina, 2001–2002.

Species or group	Period			Habitat			Period $\times$ habitat		
	<i>F</i>	df	<i>P</i>	<i>F</i>	df	<i>P</i>	<i>F</i>	df	<i>P</i>
All birds	1.00	3,162	0.40	49.71	1,22	<0.001	0.66	3,162	0.58
Forest interior species	4.94	3,162	0.003	24.05	1,22	<0.001	0.83	3,162	0.48
Forest-edge species	2.10	3,162	0.10	60.16	1,22	<0.001	0.50	3,162	0.68
Field-edge species	27.55	3,162	<0.001	85.05	1,22	<0.001	27.90	3,162	<0.001
Blue-gray Gnatcatcher	14.08	3,162	<0.001	42.82	1,22	<0.001	5.80	3,162	0.001
Carolina Wren	9.44	3,162	<0.001	83.17	1,22	<0.001	1.76	3,162	0.16
Tufted Titmouse	12.78	3,162	<0.001	18.70	1,22	<0.001	2.22	3,162	0.088
Northern Cardinal	4.60	3,162	0.004	32.76	1,22	<0.001	0.60	3,162	0.61
Northern Parula	9.63	3,162	<0.001	19.43	1,22	<0.001	2.65	3,162	0.052
White-eyed Vireo	1.82	3,162	0.15	30.56	1,22	<0.001	1.49	3,162	0.22

Gnatcatcher, Carolina Wren, Tufted Titmouse, Northern Cardinal, and Northern Parula differed among periods, but no consistent patterns were evident, as seasonal use varied considerably by species or group (Table 1, Fig. 1).

Interactions between period and habitat type existed for field-edge birds, Blue-gray Gnatcatcher, and Northern Parula (Table 1). Field-edge birds were detected most often during spring and fall migration and primarily in gap-edge habitat (Fig. 1). The greatest proportion of forest detections of field-edge birds occurred during the postbreeding period. The Blue-gray Gnatcatcher was most abundant in gap-edge habitat during all periods, but forest detections decreased to almost zero during fall migration (Fig. 1). Northern Parula used both gap-edge and forest habitat during spring migration and the breeding period, but almost all detections were in gap-edge during the postbreeding period and fall migration (Fig. 1).

Mist Netting.—From April through October in 2001 and 2002, we captured 1,476 birds representing 56 species. We captured 55 species in gap and edge habitat, and 26 species in forest habitat across all periods. We captured more individuals in the gaps and at their edges than in the surrounding forest during all periods for all bird groups and individual species except the Carolina Wren, which was captured more frequently at edge or forest habitats than gaps during all periods (Table 2, Fig. 2). Number of captures differed among periods for all groups and species analyzed except Kentucky Warbler and Northern Cardinal, with most

groups being most frequently captured during spring migration (Table 2, Fig. 2).

There was an interaction between period and habitat type, indicating a seasonal shift in habitat use, for all birds, forest-interior birds, forest-edge birds, field-edge birds, Black-throated Blue Warbler, Carolina Wren, Hooded Warbler, Kentucky Warbler, and White-eyed Vireo (Table 2). Some species (e.g., forest-interior specialists and Kentucky Warbler) shifted from gap during spring migration to edge during the breeding period and back to gap habitat after the breeding period (Fig. 3). Forest-edge birds were most abundant in the gap habitat during spring and fall migration, but both gap and edge were used equally during the breeding and postbreeding periods. Total mist-net captures tended to shift slightly between gap and edge habitat (gap during spring and fall migratory periods, edge during breeding and postbreeding), with forest captures representing just a small proportion of captures during each period. The highest proportion of forest captures, however, occurred during the breeding period (Fig. 3). Forest-interior birds, forest-edge birds, Carolina Wren, and Hooded Warbler used forested habitat most during the breeding period (Fig. 3).

DISCUSSION

We observed and captured more birds in gap and gap-edge habitat than in the surrounding mature forest during all bird-use periods. Generally, bird detections in edge habitat were more similar to detections in gap habitat than mature forest habitat. The Carolina Wren was

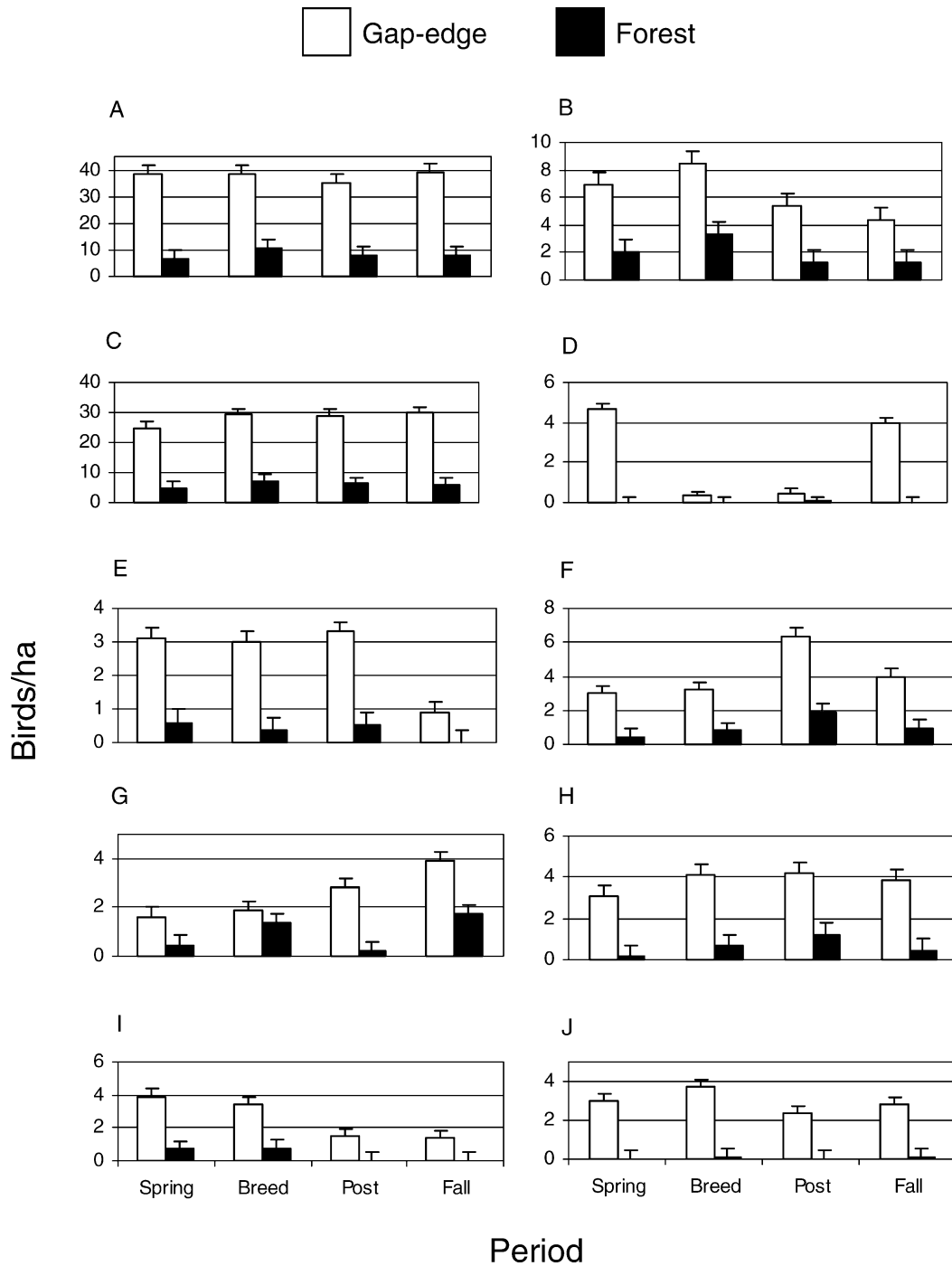


FIG. 1. Seasonal plot counts (mean birds/ha) for gap-edge (open bars) and forest habitats (filled bars), with standard error bars (2001 and 2002 in South Carolina). (A) all birds, (B) forest-interior species, (C) forest-edge species, (D) field-edge species, (E) Blue-gray Gnatcatcher, (F) Carolina Wren, (G) Tufted Titmouse, (H) Northern Cardinal, (I) Northern Parula, and (J) White-eyed Vireo.

TABLE 2. Effects of period (spring migration, breeding, postbreeding, fall migration), habitat (gap, edge, forest), and the period $\times$ habitat interaction (ANOVA) on the number of mist-net captures for bird species/groups in a bottomland hardwood forest in South Carolina, 2001–2002.

Species or group	Period			Habitat			Period $\times$ habitat		
	F	df	P	F	df	P	F	df	P
All birds	36.93	3,33	<0.001	43.99	2,33	<0.001	16.05	6,33	<0.001
Forest-interior species	21.87	3,33	<0.001	19.62	2,33	<0.001	6.82	6,33	<0.001
Forest-edge species	15.27	3,33	<0.001	22.45	2,33	<0.001	4.06	6,33	0.004
Field-edge species	36.94	3,33	<0.001	21.38	2,33	<0.001	7.37	6,33	<0.001
Black-throated Blue Warbler	8.64	1,66	0.005	17.91	2,66	<0.001	3.59	2,66	0.033
Carolina Wren	3.85	3,132	0.011	9.64	2,132	<0.001	1.96	6,132	0.076
Hooded Warbler	6.86	3,132	<0.001	14.73	2,132	<0.001	1.96	6,132	0.075
Kentucky Warbler	2.27	2,99	0.11	7.70	2,99	<0.001	5.50	4,99	<0.001
Northern Cardinal	2.25	3,132	0.085	12.65	2,132	<0.001	1.01	6,132	0.42
White-eyed Vireo	5.05	3,132	0.002	22.86	2,132	<0.001	1.83	6,132	0.098

the only species to show a distinct forest/edge preference, based on mist-netting captures. Other studies have reported more bird activity in early successional habitats than mature forest, including migrating foliage gleaning insectivores (Willson et al. 1982, Blake and Hoppes 1986, Martin and Karr 1986, Kilgo et al. 1999), breeding birds (Smith and Dallman 1996, Germaine et al. 1997, King et al. 2001, Moorman and Guynn 2001), and postbreeding birds (Anders et al. 1998; Vega Rivera et al. 1998, 1999, 2003; Pagen et al. 2000). Migrating birds also may prefer forest-edge habitat to forest-interior habitat during fall migration (Rodewald and Brittingham 2002). Other researchers have found that individual species, including Hooded Warbler (Annand and Thompson 1997, Robinson and Robinson 1999), Carolina Wren (Robinson and Robinson 1999, Moorman and Guynn 2001), and White-eyed Vireo (Robinson and Robinson 1999, Moorman and Guynn 2001) use regenerating group-selection openings more than mature forest during the breeding period. Hooded Warblers nest (Moorman et al. 2002) and forage (Kilgo 2005) in the mature forest understory on our site, but often were seen foraging in the gap habitat during all periods, and with young in gap habitat during the postbreeding period (LTB, pers. obs.).

It is possible that we captured more birds in gap habitat than forest habitat because of differences in habitat structure (Remsen and Good 1996). Birds using the low vegetation within the gaps were more available for sampling with a 3-m tall net than birds in the mature forest. However, our plot counts corroborated our mist-net data; they sampled both the understory and canopy, and also detected more birds using gap habitat than mature-forest habitat. Plot counts included birds using the immediate edge of gaps, a mix of habitat types and vegetation structures, which may have attracted forest-interior birds more than the actual gap center. Ease of detection of birds in gaps during plot counts likely was lower than in the forest because of the dense vegetation in the gaps and our estimates of bird use of gaps may be conservative.

While most birds used gap and edge habitat more than forested habitat during all periods, we also detected a seasonal shift in habitat use for several groups, as evidenced by interac-

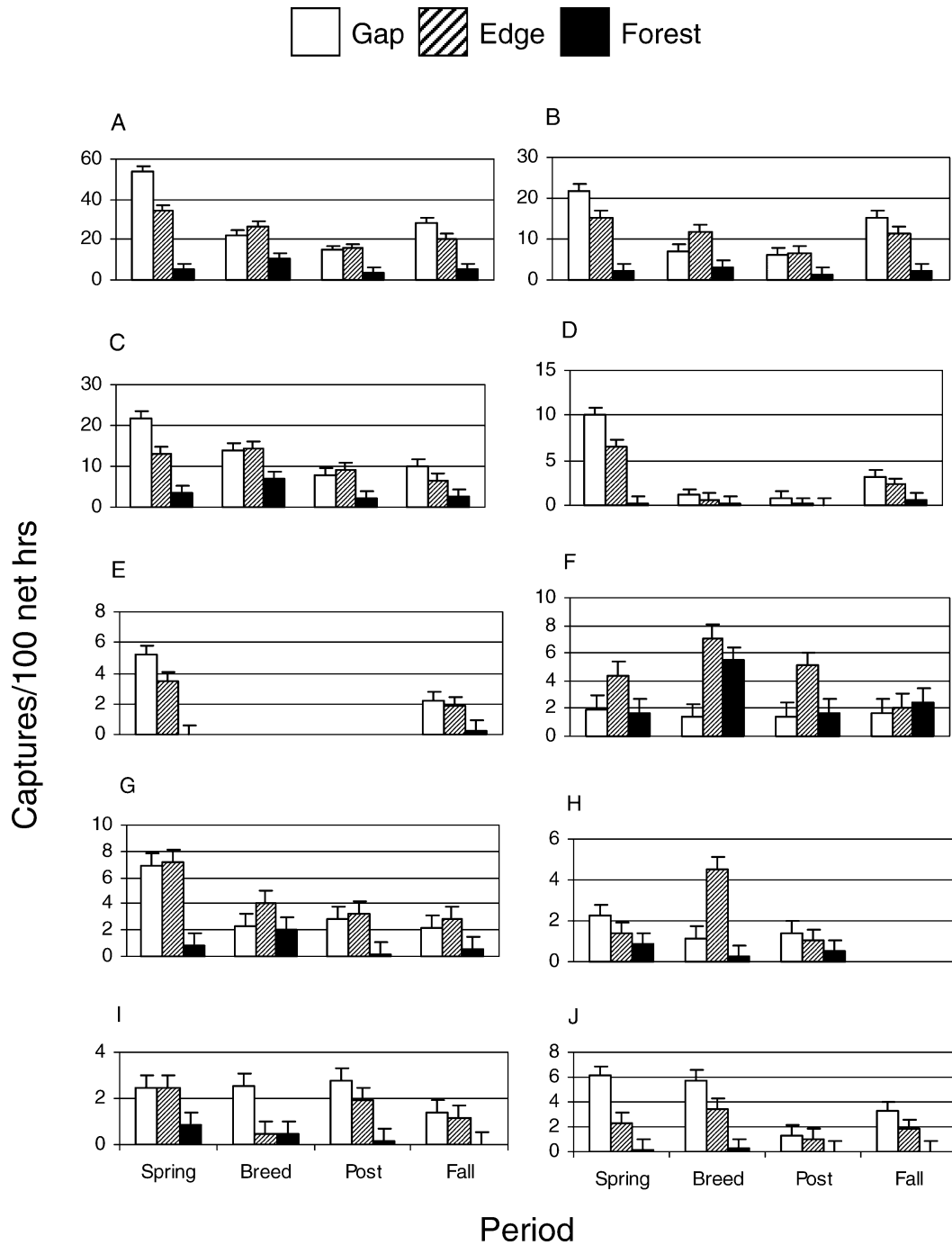


FIG. 2. Mean bird captures/100 net hrs for each habitat and period with standard error bars (2001 and 2002 in South Carolina). (A) all birds, (B) forest-interior species, (C) forest-edge species, (D) field-edge species, (E) Black-throated Blue Warbler, (F) Carolina Wren, (G) Hooded Warbler, (H) Kentucky Warbler, (I) Northern Cardinal, and (J) White-eyed Vireo.

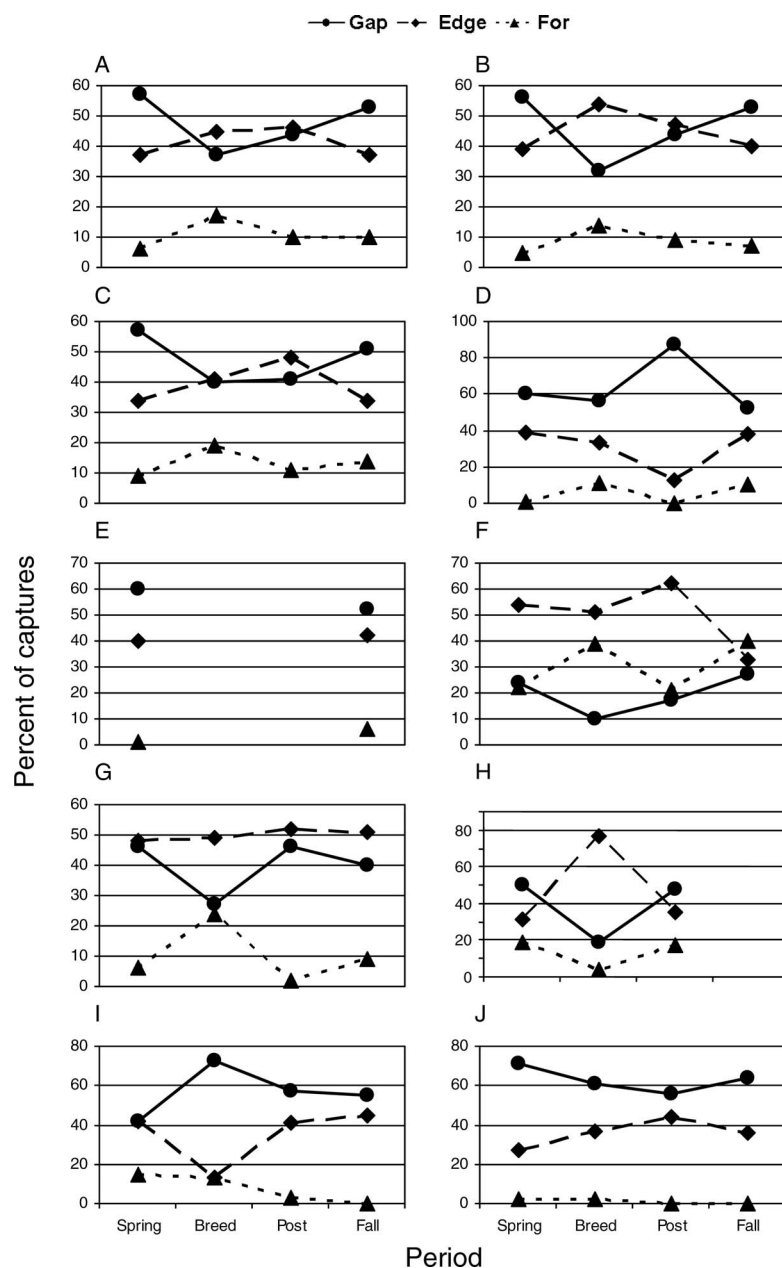


FIG. 3. Percent of mist-net captures per period occurring in each habitat type (gap, edge, forest) in a bottomland forest (2001 and 2002 in South Carolina). (A) all birds, (B) forest-interior species, (C) forest-edge species, (D) field-edge species, (E) Black-throated Blue Warbler, (F) Carolina Wren, (G) Hooded Warbler, (H) Kentucky Warbler, (I) Northern Cardinal, and (J) White-eyed Vireo.

tions between period and habitat; the relative proportions of gap, edge, and forest captures varied among periods. Generally, bird use of gap and edge habitats was highest during

spring and fall migration, while use of forested habitat tended to be greatest during the breeding period and lowest during the migratory periods. Other research has documented

seasonal shifts in habitat use between the breeding and postbreeding periods, particularly as fledgling birds moved from forested habitat into early- and mid-successional habitats (Anders et al. 1998; Vega Rivera et al. 1998, 2003; Pagen et al. 2000), possibly in search of greater cover or more abundant food resources. Regenerating forest canopy gaps may provide a necessary habitat type for birds during seasons of increased mobility.

Gap interiors were not only densely vegetated, but also contained early successional fruiting species (e.g., winged sumac [*Rhus copallina*] and blackberry), while other fruiting species such as poison ivy (*Toxicodendron radicans*) and hawthorn (*Crataegus* spp.) were common at the immediate gap edge (LTB, pers. obs.). We observed omnivorous birds eating fruits in gaps, including American beautyberry (*Callicarpa americana*), flowering dogwood (*Cornus florida*), grape (*Vitis* sp.), hawthorn, poison ivy, and winged sumac (LTB, pers. obs.). Fruit typically is most abundant from late summer through early fall (McCarty et al. 2002). Willson et al. (1982) reported that avian frugivores preferentially visited natural forest openings during migratory periods, even when these gaps provided no more fruit than surrounding forest habitat. We did not, however, find a corresponding shift in habitat use for omnivorous species such as Northern Cardinal, suggesting that birds were meeting their nutritional needs without closely following seasonal fruit availability.

Birds used regenerating canopy gaps more than mature forested habitat during all periods. Bird habitat use shifted slightly from gaps during spring migration to forest during the breeding period, then back to gaps during the postbreeding period and fall migration. Reasons for these habitat selections and seasonal shifts, however, remain speculative. It is possible that omnivorous birds use canopy gaps more during periods of high fruit availability, as canopy gaps are known for their high fruit abundance (Levey 1990). However, fruit production within our canopy gaps was relatively low and highly seasonal, with no fruit available during spring, one of the periods of highest bird use. We suspect birds may select regenerating canopy gaps for the protection offered by these densely vegetated ar-

reas, particularly during periods of vulnerability, such as during migration when birds move through unfamiliar areas and during the post-fledging period when young are more vulnerable to predators. Alternatively, birds could be tracking seasonal changes in the abundance of arthropod food resources, if the relative abundance of arthropods in gaps and forest habitat changes through the year. Additional work is needed to assess the relative importance of vegetation structure and arthropod abundance in affecting seasonal avian habitat use in southeastern forests.

The creation of 0.13- to 0.5-ha canopy gaps can increase habitat diversity within mature bottomland hardwood forest, thereby attracting a greater number of foraging, breeding, and migrating birds. This practice may be particularly beneficial in stands with a sparse understory because of dense canopy closure, a condition common to the mid-successional forests that dominate the southeastern United States. Our gaps did not impact reproductive success of Hooded Warblers nesting in the surrounding forest (Moorman et al. 2002), probably because of the extensive amount of forest cover in the landscape (i.e., the extent of forest fragmentation is low). Further, Robinson and Robinson (1999) noted that long-term effects of small-scale canopy gaps on the forest bird community are unlikely because the regenerating forest matures and returns to pre-harvest conditions in a relatively short time. When the gaps we studied were 2–5 years old (Kilgo et al. 1999, Moorman and Guynn 2001), their contrast with the surrounding forest, in terms of vegetation height and structure, was dramatic. During the current study, the gaps were 7–8 years old and the contrast was beginning to blur, with many gaps more closely resembling the surrounding forest than 3-year-old gaps; some saplings exceeded 10 m in height.

Group-selection timber harvest could allow generation of income concurrent with an increase in habitat diversity, especially in forests where rates of natural canopy-gap creation have been altered by prior human disturbance (e.g., fire suppression, even-aged timber harvest, altered flooding regimes). Pashley and Barrow (1993) recommended a management regime that mimics natural disturbance to maintain habitat heterogeneity. Our results

highlight the importance of this recommendation, as birds used both forested and early successional habitat at different times during the year.

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LITERATURE CITED

- ANDERS, A. D., J. FAABORG, AND F. R. THOMPSON, III. 1998. Postfledging dispersal, habitat use, and home-range size of juvenile Wood Thrushes. *Auk* 115:349–358.
- ANNAND, E. M. AND F. R. THOMPSON, III. 1997. Forest bird response to regeneration practices in central hardwood forests. *Journal of Wildlife Management* 61:159–171.
- BLAKE, J. G. AND W. G. HOPPE. 1986. Influence of resource abundance on use of tree-fall gaps by birds in an isolated woodlot. *Auk* 103:328–340.
- CANHAM, C. D., J. S. DENSLER, W. J. PLATT, J. R. RUNKLE, T. A. SPIES, AND P. S. WHITE. 1990. Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. *Canadian Journal of Forest Research* 20:620–631.
- EHRlich, P. R., D. S. DOBKIN, AND D. WHEYE. 1988. *The birder's handbook: a field guide to the natural history of North American birds*. Simon and Schuster, New York, USA.
- GERMAINE, S. S., S. H. VESSEY, AND D. E. CAPEN. 1997. Effects of small forest openings on the breeding bird community in a Vermont hardwood forest. *Condor* 99:708–718.
- HAMEL, P. B. 1992. *Land manager's guide to the birds of the South*. The Nature Conservancy, Chapel Hill, North Carolina, USA.
- HOLMES, R. T., R. E. BONNEY, JR., AND S. W. PACALA. 1979. Guild structure of the Hubbard Brook bird community: a multivariate approach. *Ecology* 60: 512–520.
- HUNTER, W. C., D. A. BUEHLER, R. A. CANTERBURY, J. L. CONFER, AND P. B. HAMEL. 2001. Conservation of disturbance-dependent birds in eastern North America. *Wildlife Society Bulletin* 29:440–455.
- KILGO, J. C. 2005. Harvest-related edge effects on prey availability and foraging of Hooded Warblers in a bottomland hardwood forest. *Condor* 107:626–635.
- KILGO, J. C., K. V. MILLER, AND W. P. SMITH. 1999. Effects of group-selection timber harvest in bottomland hardwoods on fall migrant birds. *Journal of Field Ornithology* 70:404–413.
- KING, D. I., R. M. DEGRAAF, AND C. R. GRIFFIN. 2001. Productivity of early successional shrubland birds in clearcuts and groupcuts in an eastern deciduous forest. *Journal of Wildlife Management* 65:345–350.
- LEVEY, D. J. 1990. Habitat-dependent fruiting behaviour of an understory tree, *Miconia centrodesma*, and tropical treefall gaps as keystone habitats for frugivores in Costa Rica. *Journal of Tropical Ecology* 6:409–420.
- MARTIN, T. E. AND J. R. KARR. 1986. Patch utilization by migrating birds: resource oriented? *Ornis Scandinavia* 17:165–174.
- MCCARTY, J. P., D. J. LEVEY, C. H. GREENBERG, AND S. SARGENT. 2002. Spatial and temporal variation in fruit use by wildlife in a forested landscape. *Forest Ecology and Management* 164:277–291.
- MOORE, F. R., S. A. GAUTHREAUX, JR., P. KERLINGER, AND T. R. SIMONS. 1993. Stopover habitat: management implications and guidelines. Pages 58–69 in *Status and management of neotropical migratory birds* (D. Finch and P. Stangel, Editors). General Technical Report RM-229. USDA, Forest Service, Fort Collins, Colorado, USA.
- MOORMAN, C. E. AND D. C. GUYNN, JR. 2001. Effects of group-selection opening size on breeding bird habitat use in a bottomland forest. *Ecological Applications* 11:1680–1691.
- MOORMAN, C. E., D. C. GUYNN, JR., AND J. C. KILGO. 2002. Hooded Warbler nesting success adjacent to group-selection and clearcut edges in a southeastern bottomland forest. *Condor* 104:366–377.
- PAGEN, R. W., F. R. THOMPSON, III, AND D. E. BURNHANS. 2000. Breeding and post-breeding habitat use by forest migrant songbirds in the Missouri Ozarks. *Condor* 102:738–747.
- PASHLEY, D. N. AND W. C. BARROW. 1993. Effects of land use practices on neotropical migratory birds in bottomland hardwood forests. Pages 315–320 in *Status and management of neotropical migratory birds* (D. Finch and P. Stangel, Editors). General Technical Report RM-229. USDA, Forest Service, Fort Collins, Colorado, USA.
- PETIT, D. R. 2000. Habitat use by landbirds along Neartic-neotropical migration routes: implications for conservation of stopover habitats. *Studies in Avian Biology* 20:15–33.
- PYLE, P. 1997. *Identification guide to North American passerines*. Part I. Slate Creek Press, Bolinas, California, USA.
- REMSEN, JR., J. V. AND D. A. GOOD. 1996. Misuse of data from mist-net captures to assess relative abundance in bird populations. *Auk* 113:381–398.
- ROBINSON, S. K. AND R. T. HOLMES. 1982. Foraging

- behavior of forest birds and the relationships among search tactics, diet, and habitat structure. *Ecology* 63:1918–1931.
- ROBINSON, W. D. AND S. K. ROBINSON. 1999. Effects of selective logging on forest bird populations in a fragmented landscape. *Conservation Biology* 13:58–66.
- RODEWALD, P. G. AND M. C. BRITTINGHAM. 2002. Habitat use and behavior of mixed species landbird flocks during fall migration. *Wilson Bulletin* 114: 87–98.
- SAS INSTITUTE, INC. 1990. SAS user's guide. 6. SAS Institute, Inc., Cary, North Carolina, USA.
- SMITH, R. AND M. DALLMAN. 1996. Forest gap use by breeding Black-throated Green Warblers. *Wilson Bulletin* 108:588–591.
- VEGA RIVERA, J. H., W. J. MCSHEA, AND J. H. RAPPOLE. 2003. Comparison of breeding and postbreeding movements and habitat requirements for the Scarlet Tanager (*Piranga olivacea*) in Virginia. *Auk* 120:632–644.
- VEGA RIVERA, J. H., W. J. MCSHEA, J. H. RAPPOLE, AND C. A. HAAS. 1999. Postbreeding movements and habitat use of adult Wood Thrushes in northern Virginia. *Auk* 116:458–466.
- VEGA RIVERA, J. H., J. H. RAPPOLE, W. J. MCSHEA, AND C. A. HAAS. 1998. Wood Thrush postfledging movements and habitat use in northern Virginia. *Condor* 100:69–78.
- WATT, A. S. 1947. Pattern and process in the plant community. *Journal of Ecology* 35:1–22.
- WILLSON, M. F., E. A. PORTER, AND R. S. CONDIT. 1982. Avian frugivore activity in relation to forest light gaps. *Caribbean Journal of Science* 18:1–6.

IAPPENDIX. Observed bird species and their habitat group associations. Species included were detected by plot counts or mist-netting at least once (South Carolina, 2001–2002).

Species	Scientific name	Habitat group
Turkey Vulture	<i>Cathartes aura</i>	field edge
Red-shouldered Hawk	<i>Buteo lineatus</i>	forest edge
Mourning Dove	<i>Zenaida macroura</i>	field edge
Yellow-billed Cuckoo	<i>Coccyzus americanus</i>	forest edge
Barred Owl	<i>Strix varia</i>	forest interior
Ruby-throated Hummingbird	<i>Archilochus colubris</i>	forest edge
Red-headed Woodpecker	<i>Melanerpes erythrocephalus</i>	forest edge
Red-bellied Woodpecker	<i>Melanerpes carolinus</i>	forest edge
Downy Woodpecker	<i>Picoides pubescens</i>	forest edge
Hairy Woodpecker	<i>Picoides villosus</i>	forest interior
Northern Flicker	<i>Colaptes auratus</i>	forest edge
Pileated Woodpecker	<i>Dryocopus pileatus</i>	forest interior
Eastern Wood-Pewee	<i>Contopus virens</i>	forest edge
Acadian Flycatcher	<i>Empidonax virens</i>	forest interior
Eastern Phoebe	<i>Sayornis phoebe</i>	forest edge
Great Crested Flycatcher	<i>Myiarchus crinitus</i>	forest edge
White-eyed Vireo	<i>Vireo griseus</i>	forest edge
Yellow-throated Vireo	<i>Vireo flavifrons</i>	forest edge
Blue-headed Vireo	<i>Vireo solitarius</i>	forest interior
Red-eyed Vireo	<i>Vireo olivaceus</i>	forest interior
Blue Jay	<i>Cyanocitta cristata</i>	forest edge
American Crow	<i>Corvus brachyrhynchos</i>	forest edge
Fish Crow	<i>Corvus ossifragus</i>	forest edge
Carolina Chickadee	<i>Poecile carolinensis</i>	forest edge
Tufted Titmouse	<i>Baeolophus bicolor</i>	forest edge
White-breasted Nuthatch	<i>Sitta carolinensis</i>	forest edge
Brown-headed Nuthatch	<i>Sitta pusilla</i>	forest edge
Carolina Wren	<i>Thryothorus ludovicianus</i>	forest edge
Blue-gray Gnatcatcher	<i>Poliophtila caerulea</i>	forest edge
Veery	<i>Catharus fuscescens</i>	forest interior
Gray-cheeked Thrush	<i>Catharus minimus</i>	forest interior
Bicknell's Thrush	<i>Catharus bicknelli</i>	forest interior
Swainson's Thrush	<i>Catharus ustulatus</i>	forest interior
Hermit Thrush	<i>Catharus guttatus</i>	forest interior
Wood Thrush	<i>Hylocichla mustelina</i>	forest interior
Gray Catbird	<i>Dumetella carolinensis</i>	field edge
Brown Thrasher	<i>Toxostoma rufum</i>	field edge

APPENDIX. Continued.

Species	Scientific name	Habitat group
Blue-winged Warbler	<i>Vermivora pinus</i>	field edge
Golden-Winged Warbler	<i>Vermivora chrysoptera</i>	forest edge
Northern Parula	<i>Parula americana</i>	forest edge
Chestnut-sided Warbler	<i>Dendroica pensylvanica</i>	field edge
Magnolia Warbler	<i>Dendroica magnolia</i>	forest interior
Black-throated Blue Warbler	<i>Dendroica caerulescens</i>	forest interior
Yellow-rumped Warbler	<i>Dendroica coronata</i>	forest edge
Black-throated Green Warbler	<i>Dendroica virens</i>	forest interior
Pine Warbler	<i>Dendroica pinus</i>	forest edge
Prairie Warbler	<i>Dendroica discolor</i>	field edge
Black-and-white Warbler	<i>Mniotilta varia</i>	forest interior
American Redstart	<i>Setophaga ruticilla</i>	forest interior
Worm-eating Warbler	<i>Helmitheros vermivorum</i>	forest edge
Swainson's Warbler	<i>Limothlypis swainsonii</i>	forest interior
Ovenbird	<i>Seiurus aurocapilla</i>	forest interior
Northern Waterthrush	<i>Seiurus noveboracensis</i>	forest interior
Louisiana Waterthrush	<i>Seiurus motacilla</i>	forest interior
Kentucky Warbler	<i>Oporornis formosus</i>	forest interior
Common Yellowthroat	<i>Geothlypis trichas</i>	field edge
Hooded Warbler	<i>Wilsonia citrina</i>	forest interior
Canada Warbler	<i>Wilsonia canadensis</i>	forest interior
Yellow-breasted Chat	<i>Icteria virens</i>	field edge
Summer Tanager	<i>Piranga rubra</i>	forest edge
Scarlet Tanager	<i>Piranga olivacea</i>	forest interior
Eastern Towhee	<i>Pipilo erythrophthalmus</i>	field edge
Northern Cardinal	<i>Cardinalis cardinalis</i>	forest edge
Rose-breasted Grosbeak	<i>Pheucticus ludovicianus</i>	forest interior
Indigo Bunting	<i>Passerina cyanea</i>	field edge
Common Grackle	<i>Quiscalus quiscula</i>	field edge
Brown-headed Cowbird	<i>Molothrus ater</i>	forest edge